NOTES ON THE FEEDING MECHANISM AND ON INTESTINAL RESPIRATION IN CHÆTOPTERUS VARIOPEDATUS[1]

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A healthy *Chætopterus* introduced into a glass tube rapidly lines this with a parchment-like secretion. One individual, after living in such a tube for two weeks, extended the lining beyond the aperture of the tube at one end. The prolongation was sharply constricted, showed successive thickened rings, and terminated in an expanded rim; it was, in fact, an exaggeration of the constriction at the end of a normal tube.

The tube current in such a preparation, as is well known, enters the tube anteriorly and leaves posteriorly, maintained by the rhythmic beating of the fans on segments 14, 15, and 16. It is weak ventral to the animal, but strong dorsally, and is directed under the arch formed by the long parapodia of segment 12.

This main tube current provides the food supply, the nature of which has been described by Enders (1909). The collecting mechanism has been described by several authors as follows: the broad ciliated buccal funnel collects directly from an extensive antero-ventral field; in addition, ciliated grooves on the dorsal side of the thorax collect from the tube current. To demonstrate this when the animal is removed from its tube, food particles must be supplied by dropping them onto the thorax from a pipette.

Such particles are collected in a mucoid stream into grooves along the inner edge of the arch formed by the parapodia of segment 12, and pass from this anteriorly in a median groove. Particles which happen to fall on the ventral face of the thorax are passed in laterally moving streams dorsally, between some of the posterior parapodia—being thus brought into the dorsal collecting field. The median dorsal groove does not lead directly into the mouth, but ends blindly in a dilatation posterior to the dorsal lip overhanging the mouth (Fig. 1). The wall round the terminal dilatation is thickened and raised, and forms a three-lobed prominence. The anatomical details of the structure of the groove have been given by Joyeux-Laffuie (1890).

[1] The following notes were made during a visit to the Marine Biological Laboratory at Woods Hole during August and September, 1929. The author wishes to thank Dr. F. R. Lillie for his interest and assistance.

In describing the transference of food from the groove into the mouth, Enders stated that "the lip of the buccal funnel is drawn backwards, and the ciliary groove, which now extends beyond the dorsal border of the mouth, permits the granules to fall directly upon the ventral lip of the funnel." Described in more detail, the complete course of events is as follows.

While the food is passing forward in the groove, the anterior edge of the dorsal lip is reflected posteriorly until its tip comes into contact with the wall of the terminal dilatation of the groove (Fig. 2). To aid this, the posterior half of the lip is depressed by ventral muscular contractions centering in two areas. One of these is immediately anterior to the end of the groove; the other forms a pit within the tissue of the lip. These two contractions result in the formation of a deep transverse groove between the anterior end of the dorsal groove and the anterior edge of the lip, arched over by the lip when this is reflected.

A further contraction now follows, as a result of which the exposed surface of the reflected lip becomes depressed in the median-sagittal line so as to form a deep longitudinal groove, which is a direct continuation of the groove on the thorax; the food particles can now pass from one to the other without any interruption or obstruction (Fig. 3).

When the food has passed over the groove and into the mouth, the lip is relaxed and returns to its position of rest. If it happens that the food is removed before it reaches the anterior end of the thorax, the lip does not complete this normal cycle of action, but is relaxed at once.

The stimulus which excites this reflex is apparently the presence of solid particles in the food groove. In addition to this mechanical sensitivity there may be some sense of chemical discrimination also, as the animals often discard carmine or other non-nutritive particles.

The lip action can be induced experimentally in the following manner. A fine brush from which all but a few hairs have been removed is drawn slowly along the groove from the posterior end, and the lip responds as described above: the advantage of using such a type of stimulation is that one point only of the groove is stimulated at any one moment. While the brush is in the posterior end of the groove there is no response, but when it reaches approximately the level of the third or fourth setigerous parapodium, reflection of the lip begins. The exact extent of the anterior sensitive area varies, but it seems to be not more than one-fifth of the total length of the groove. The lip is reflected before the food reaches it,—it acts at such a time, in fact, that when the first granules reach the end of the thoracic groove, the groove on the lip is just ready to receive them. Stimulation of the anterior raised termination of the groove causes immediate response irrespective of whether or not the groove itself has been stimulated previously.

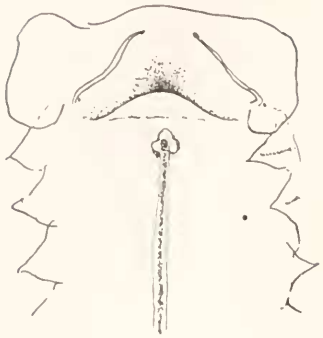

FIG. 1.

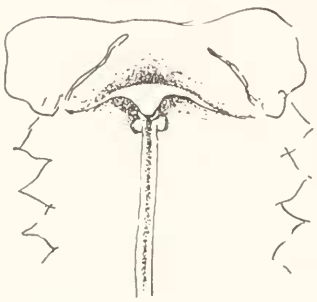

FIG. 2.

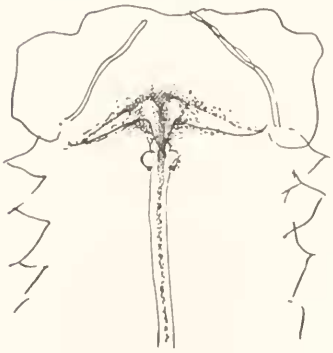

FIG. 3.

FIG. 1. Anterior end, dorsal view, showing lip in position of rest. (Diagrammatic.)

FIG. 2. The same, with lip reflected posteriorly.

FIG. 3. Lip reflected and grooved longitudinally ready to receive the food stream from the thoracic groove.

In connection with this reflex action it is of interest to compare a figure given by Joyeux-Laffuie of the nervous system of *Chætopterus*. He shows a pair of nerves arising from the dorsal region of the circumœsophageal ring and extending over approximately the anterior half of the setigerous thoracic segments—thus corresponding more or less in their distribution with the extent of the sensitive area.

Observations on intestinal respiration were made on individuals which had recently regenerated some posterior segments. Such new somites are transparent and free from pigment, and are particularly favorable for this purpose.

Stephenson (1913) mentions *Chætopterus* in his paper on intestinal respiration and records an in-going current at the anus, but adds that no anti-peristaltic contraction of the gut was seen. Such contractions have, however, been seen repeatedly in recently regenerated somites, though not in normal pigmented individuals. In addition to anti-peristaltic contractions, the "gulping" action recorded by Stephenson in several genera was seen at times, and there was in some cases also observed a pulsating or pumping action in the gut at some distance in front of the anus.

The simple anti-peristaltic action will be described first. It is an anteriorly moving wave of contraction passing over the alimentary canal in the few hind somites, constricting both the walls and the lumen. The number of segments over which it persists varies, but it has repeatedly been watched over at least seven segments, and occasionally over one or two more. The interval of time separating successive waves varies also, both in different individuals, and in the same individual on different occasions: in fact, the activity often ceases altogether. When active, the waves may follow each other at intervals of 4, 3, 2, or even 1½ seconds.

A regular "gulping" action was seen only rarely, though it is not uncommon to see the anus opening and closing at irregular intervals; this action is usually associated with a movement of protrusion and retraction of the posterior end of the canal. In one particularly favorable individual the "gulping" action maintained a rhythm with intervals of approximately one second, while after every three or four gulps there was a pause while a peristaltic wave passed anteriorly over a few segments.

The pumping mechanism mentioned above probably serves to reinforce the peristaltic wave: it may synchronize with the wave, or may have an independent rhythm. It is seen less frequently than the peristalsis. The action occurs about seven somites in front of the hind end, but as details vary, a few precise examples will be given.

One individual examined had seven newly regenerated somites at the hind end, all perfectly colorless and transparent. Anti-peristaltic

waves passed over the alimentary canal in the posterior segments, succeeding each other at intervals of approximately four seconds. At the same time, the gut in the fifth segment from the hind end maintained a pulsation independent of this wave, the beats occurring at intervals of about one second. In another case peristaltic waves passed forwards over the gut, and as they reached the seventh segment from the hind end and were becoming weak, they received renewed impetus and persisted through two or three segments further.

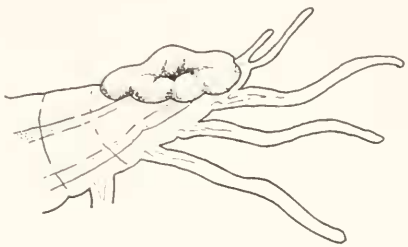

FIG. 4. Posterior end, showing the intestine protruded at anus.

The function of this anal and intestinal mechanism may be two-fold, as suggested by previous authors (see Stephenson, 1913 and 1930).

In the first place, the in-going anal current may be respiratory: *Chætopterus* has no special respiratory organs, and there are several features which support the suggestion that the anus may play a part in respiration. In the present case all the observations were made in aquaria, hence, although the aëration was maintained as efficiently as possible, it was not normal. However, it is known that in the natural situation the animal often protrudes its hind end from the tube. Further than this, there is a terminal swelling on the alimentary canal which is protrusible, and which, when everted, forms a rosette-shaped protrusion around the anus (Fig. 4). When retracted, the termination of the canal appears compressed and much folded. There is also, as described by Enders, a longitudinal groove in the intestine in which the cells are distinguished by their stronger cilia and by the absence of green granules. In the oligochætes similar grooves are associated with an in-going respiratory current, and the same explanation may perhaps be true here.

In the second place, the muscular activity of the intestinal wall may be for the purpose of propulsion of blood in a peri-enteric sinus or plexus: such a peri-enteric plexus exists in *Chætopterus* according to Probst (1929).

Summary

1. The food of *Chætopterus* is transferred from the dorsal thoracic groove to the mouth by the temporary adaptation of the dorsal lip to form a conducting channel leading directly into the mouth from the blind anterior termination of the groove.

2. This reaction of the dorsal lip can be induced by mechanical stimulation of the anterior part of the dorsal groove.

3. Clear and colorless somites which have been regenerated recently at the hind end of a *Chætopterus* demonstrate the occurrence of antiperistaltic contractions in the alimentary canal of the hind segments; such individuals also show a "gulping" action at the anus, and an accessory pumping mechanism in the walls of the intestine amplifying the peristaltic contractions.

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